

Community composition and size structure of murid rodents in relation to the biogeography of the Japanese archipelago

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We investigated the geographical patterns of community composition and size structure of murid rodent assemblages in Japan. Rodent faunal composition showed three biogeographic zones in the studied area (Hokkaido, northern Honshu and southern Honshu), which are characterized by endemic species or genera. There was a large discrepancy between distribution patterns of murine species, which are generalist and widespread in Japan, and arvicoline species, which are more specialized and locally restricted. We also found a strong degree of nestedness of the murid rodent fauna, i.e. smaller faunas were subsets of larger ones, which is typical of relict fauna. The structure of murid rodent assemblages was studied using the size and shape of the lower incisor, in order to test for the effect of interspecific competition on community-wide patterns. We used two different approaches: one tests for regularity in the size structure of the community (Barton and David test), and the other one tests for minimum mean overlap size in the community between species (randomization procedure). There was no congruence between the results of the two tests: we did not find any case of regular size structure, whereas mean size overlaps were minimum or even zero in about half of the cases studied. Thus, the evolution of rodent communities on islands seems to be characterized by minimization of size overlaps, perhaps as a result of interspecific competition. Also, the reduction of island area, which is correlated with a decrease in species richness, is accompanied by an increase in Hutchinsonian size ratios and a decrease in the total size range of the community. These patterns may be linked to the reduced diversity of environmental resources on islands.

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The Japanese archipelago is a long chain of islands located off the eastern coast of Asia, that collectively cover a surface of 377000 km², between 120°E and 150°E and 22°N and 45°N. Except for the Ryukyu islands in south, which were excluded from this study, most of this archipelago falls within the Palearctic region as described by Corbet (1978). The Japanese archipelago comprises > 3900 islands of greatly differing area, ranging from < 1 km² to > 230000 km². In addition, geological evidence shows that these islands

experienced various histories, some of them being connected to each other or to the adjacent Asiatic mainland during times of sea-level lowering, while others remained isolated during the whole Quaternary (Fujii 1990, Oshima 1990).

The climate of Japan is a mid-latitude oceanic climate, with relatively high precipitation and a small annual mean temperature variation, and varies from cool temperate in the north to tropical in south. The vegetation types of Japan separate four main biogeo-

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graphic regions (Fukui 1977, Dobson 1994). The first is Hokkaido where a subboreal coniferous forest is the main vegetation although some montane forests occur in high elevations. In northern Honshu, the dominant vegetation is a temperate deciduous broadleaf forest while in southern Honshu the vegetation is dominated by a warm-temperate evergreen broadleaf forest. The Ryukyu islands are characterised by a tropical rain forest.

Japanese rodents represent 21.1% of all the terrestrial mammalian species from Japan (Nowak and Paradiso 1983, Abe 1994), most of these species belonging to the Muridae (12 out of the 19 rodent species, which also include Scuriidae and Gliridae). The peculiarities of the Japanese mammalian fauna, especially its high degree of endemism, have long been recognised (Wallace 1892, Kuroda 1939). At a large scale, the current distribution of the terrestrial mammals in Japan seems to be mainly the result of selective post-glacial extinctions that were not balanced by colonisations of new species from the Asiatic mainland (Millien-Parra and Jaeger 1999). However, other factors may have greatly influence the distribution of rodent species within the Japanese archipelago.

Competition between species has been viewed as having a key role in influencing the ecological, biogeographical and evolutionary patterns of mammal communities. Brown and Wilson (1956) first proposed that species in sympatry exert competitive pressure on each other, resulting in character displacement between them. Hutchinson (1959) then suggested, based on empirical observations, that a minimum theoretical size ratio of 1.28 between two species was necessary for their coexistence. In a series of recent papers, Dayan et al. (1989, 1990) and Dayan and Simberloff (1994) showed that the size ratios between sympatric species were more equal than those produced by chance alone. They proposed that for heteromyid rodents, the ratios for the upper incisor size should be more equal than for other traits, such as body weight or skull length (Dayan and Simberloff 1994). These results were corroborated in a recent study of several rodent communities suggesting that body size was not the best axis of community size structure among rodents (Parra et al. 1999). Moreover, we hypothesised that the radius of the curvature should be a better indicator of community structure than any other dimension of the incisor, since it is also linked to resource exploitation, in addition to overall body size (Parra et al. 1999, Millien-Parra unpubl.).

The variety of climate and vegetation in Japan, combined with the different degrees of isolation, the wide range of areas of the Japanese islands, and the peculiar characteristics of the Japanese rodent species, make the Japanese archipelago an ideal ecological system to investigate the patterns of geographical variation in the composition and community structure of rodent assemblages. In addition, in order to test for the relative

impact of species size and habit on community structure, the present work examines the differentiation among the Japanese murid communities, using the lower incisor size and shape.

Material and methods

Material

The material used for this study includes 597 specimens from 17 rodent assemblages that occur in the following sites: Mt. Poroshiri, Mt. Daisetsuzan, Rishiri island, Mt. Goyo, Mt. Hayachine, Sado island, Oki island, Nikko, Harunako lake, Mt. Fuji, Mt. Takao, Mt. Odaigahara, Mt. Daisen, Kisuki-cho, Tsushima island, Tane island and Shikine island (Fig. 1). They belong to three biogeographic zones from Japan that support different faunas and floras, under various climatic regimes. In addition, they are located on islands of greatly differing area, from 4 km² (Shikine island) to 230000 km² (Honshu). All the material is stored at the National Science Museum, Tokyo.

The murid species considered belong to two subfamilies: the Murinae (*Rattus* and *Apodemus*) and the Arvicolinae (*Microtus*, *Clethrionomys* and *Phaulomys*). The list of the fauna and its geographical distribution were compiled mainly from Musser and Carleton (1993) and Abe (1994), and we followed the classification proposed in Musser and Carleton (1993), although the species status of some taxa is still controversial, especially for the genus *Rattus* (Kaneko and Murakami 1996). Introduced and commensal species such as *Rattus rattus*, *Mus musculus*, *M. caroli* and *Micromys minu-*

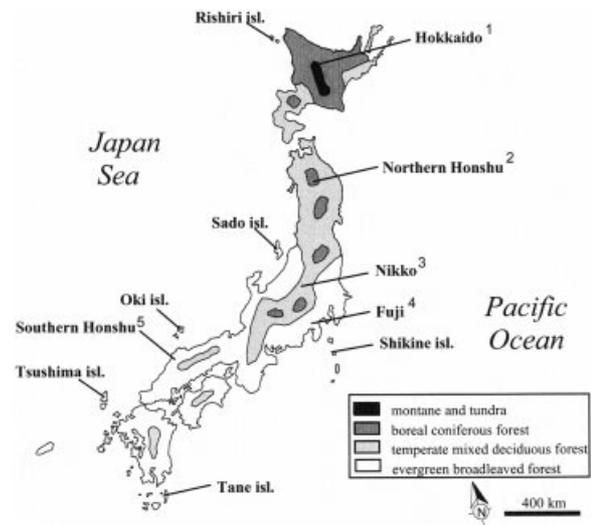


Fig. 1. Location of the eleven localities studied in the Japanese islands. 1: Mt. Poroshiri + Mt. Daisetsuzan; 2: Mt. Goyo + Mt. Hayachine; 3: Nikko + Harunako Lake; 4: Mt. Fuji + Mt. Takao; 5: Mt. Odaigahara + Mt. Daisen + Kisuki-cho.

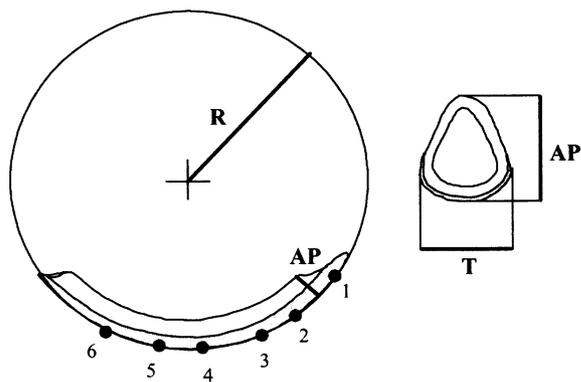


Fig. 2. Lower incisor in lateral and cross-sectional views showing the three measurements taken: antero-posterior diameter (AP), radius of curvature (R) and transverse diameter (T). Points 1 to 6 located on the anterior edge of the incisor were used to estimate the radius of curvature.

tus were not included in this analysis. *Rattus norvegicus* was considered as a native species of Japan as it is known from Quaternary fossil localities (Kowalski and Hasegawa 1976, Kawamura 1989).

Measurements

Three characters of the lower incisor were selected (Fig. 2): AP, the antero-posterior diameter, T, the transverse diameter and R, the radius of the lower incisor curvature. The two measurements AP and T were taken at the level of the incisor gap. The radius of curvature R was estimated from the coordinates of six points taken on the anterior edge of the incisor. All the measurements were taken with a drawing tube coupled with a 2D digitizer to the nearest 0.01 mm.

Sampling of communities

Studied material was collected in Japan between 1949 and 1995. A natural single species rodent population should be made up of individuals that actually coexisted in one single locality. However, this would have resulted in very small sample size for each species considered. We chose to enlarge sample size by combining several populations from different sites, and building some communities that can be made up of populations that were not necessarily collected at the same location. We thus performed one-way ANOVAs and multiple mean comparison Scheffé tests on the three size characters measured on lower incisors in order to test for the effect of site, which allowed us to make some pooling between samples collected in different sites. Three conditions were necessary to allow these combinations of samples: 1) the two sites must belong to the same biogeographic zone (i.e. Hokkaido, north-

ern Honshu or southern Honshu); 2) the two sites must be identical in term of species composition; and 3) results of Scheffé mean comparison tests must be non significant for the three size characters considered, and for all the species of the communities.

The results of these comparisons allowed us to consider eleven localities, after the combinations of some of them (Fig. 1). The locality northern Honshu (Iwate prefecture) is made up of the two sites from Mt. Goyo and Mt. Hayachine. A very small sample was collected near Harunako lake and was put together with the locality Nikko (Tochigi prefecture). Similarly, the assemblage from Mt. Takao was not different from those of Mt. Fuji (Yamanashi prefecture). The locality from southern Honshu (Shimane prefecture) is made up of the three assemblages from Mt. Odaigahara, Mt. Daisen and Kisuki-cho. Finally, the two sites from Hokkaido, Mt. Poroshiri and Mt. Daisetsuzan were put together. All the populations at the six remaining localities (Sado, Oki, Tane, Tsushima, Shikine, and Rishiri islands) remained unaltered. These poolings were made in order to increase the power of the following analyses where we concentrate on the different patterns that exist between different biogeographic zones and between different islands, for example latitudinal gradients of community structure, or the effect of island size and isolation on this structure. We did not pool samples from different islands and from different biogeographic zones (i.e. Hokkaido and small adjacent islands, northern Honshu and small adjacent islands, and southern Honshu and small adjacent islands), in order to maintain island-specific and biogeographic zone-specific responses.

Patterns of community composition

In order to quantify the overall similarity between the eleven localities considered, we computed the Simpson's similarity index following the formula $R_S = C/N$, where C is the number of species shared, and N the number of species in the smaller fauna (Simpson 1943, cited in Janson and Vegelius 1981). The matrix of Simpson indices was then subjected to a UPGMA cluster analysis, using SYSTAT for Macintosh (ver. 5.2.1).

We also used the method described in Atmar and Patterson (1993) to measure the degree of nestedness of the presence-absence matrix of the Japanese murid rodent assemblages. Nestedness is the tendency of smaller faunas to contain a subset of the species in the larger faunas. The metric used is T, the "matrix temperature", which ranges from 0° for a perfectly nested matrix to 100° for a matrix that is completely disordered. The statistical significance of the T value computed was assessed by a Monte Carlo simulation, using the "Nestedness Calculator" of Atmar and Patterson (1995).

Community structure

We used two different approaches to test for the effect of interspecific competition on community-wide patterns in the size and shape of the lower incisor. One tests for constancy of size ratios between adjacent species (Barton and David test), and the other tests for minimum mean size overlap between species pairs (randomisation test).

To test for equality of size ratios, we used Barton and David's (1956, hereafter B&D) statistic (Simberloff and Boecklen 1981, Dayan et al. 1989, 1990, Dayan and Simberloff 1994). This method tests for constancy of ratios between the mean sizes of paired size-ranked species in a community. As in Dayan and Simberloff (1994), we used the B&D statistic $G1, n$, which is the ratio of the smallest to the largest size ratio. The null hypothesis that the observed ratios do not differ from those produced by chance alone is rejected when the probability lies under the significance level.

We also used the method proposed by Loreau (1989) and adapted by Parra et al. (1999) to test for the minimisation of size overlap between adjacent species. A randomisation procedure allows the species size-distributions to shift randomly, and gives the probability of finding an overlap that is smaller than or equal to the observed value. If this probability lies under the significance level, one can reject the null hypothesis that the observed overlap is produced by chance alone. The statistic used was the mean pairwise size overlap between species, where size overlap was calculated following Levins's (1968) niche-overlap index.

Results

Between locality patterns: community composition

Similarity between murid rodent fauna

The matrix of Simpson's similarity indices between the eleven localities studied was subjected to an UPGMA analysis, and the resulting dendrogram is given in Fig. 3. The first node isolates the two localities Hokkaido and Rishiri islands from the other localities. These two localities are located in the most northerly part of Japan and support the genus *Clethrionomys*, which is absent elsewhere. The second node isolates the three islands of Tsushima, Tane and Shikine. These three islands are located in southern Japan and support impoverished rodent fauna only represented by the genera *Apodemus* and *Rattus*. Finally, the third node separates localities from the northern part of Honshu (northern Honshu and Sado island) from those of southern part (Nikko, Fuji, southern Honshu and Oki island). These two areas are differentiated by the occurrence of *Phaulomys andersoni* in the north and *P. smithii* in the south (Fig. 4).

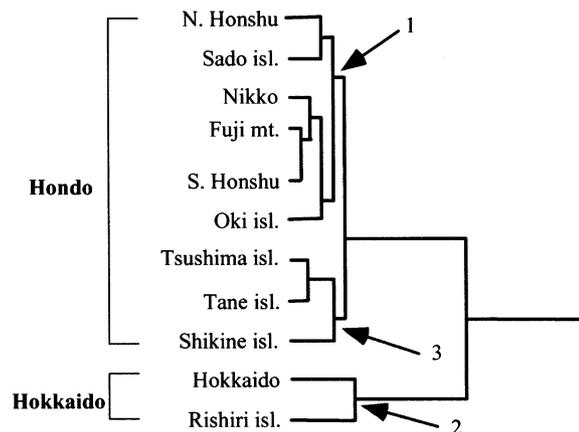


Fig. 3. Faunal similarity between the eleven localities studied depicted by a dendrogram based on Simpson similarity indices. The two biogeographic zones of Hokkaido and Honshu are well discriminated according to their rodent fauna. 1: presence of *Microtus* and *Phaulomys*; 2: presence of *Clethrionomys*; 3: absence of Arvicolinae.

Nestedness of the fauna

In order to test for the degree of nestedness of the Japanese murid rodent assemblages, we used the nestedness calculator from Atmar and Patterson (1995) which ranks localities by increasing species richness, and species by increasing occurrence frequency (Fig. 5). This program packs the matrix of presence-absence of species so as to maximise the nestedness of the fauna,

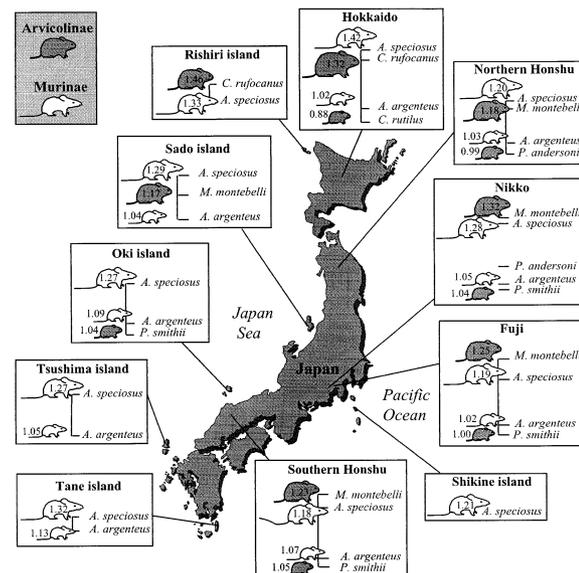


Fig. 4. Composition of the Japanese murid communities. The Murinae are widespread in Japan, while the Arvicolinae are different from one locality to another. Numbers indicate the mean size of the lower incisor antero-posterior diameter (AP), in mm. The genus *Rattus* was not considered since it is present in all localities studied and substantially larger in size than any other Japanese rodent species.

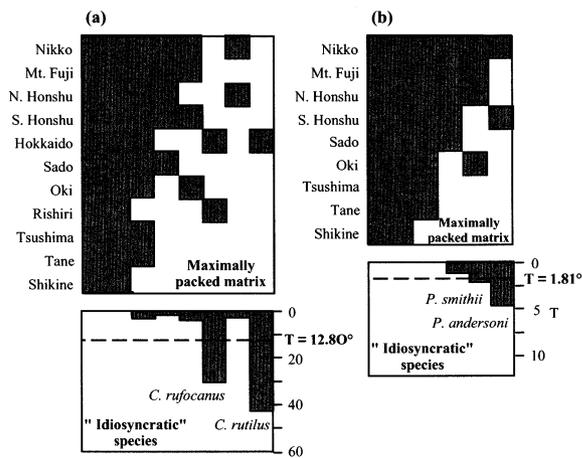


Fig. 5. Matrix of presence-absence for the eleven localities studied (a) and for a subset of nine localities from the Hondo area (all localities, except Hokkaido and Rishiri island (b)). Localities are arranged by increasing species richness, while species are arranged by increasing frequency of occurrence. The two data sets show a significant degree of nestedness, but only the nine localities subset has a very low temperature (i.e. very strong degree of nestedness). For each data set, a plot of "idiosyncratic" species scores is provided, showing the contribution of each species to the matrix temperature.

or minimise the matrix temperature. This particular calculation was used by Patterson and Atmar (1986) to describe the nested community structure of land-bridge island communities. The matrix temperature that reflects the degree of nestedness of the fauna was computed for the whole data set that included the eleven localities studied.

The resulting matrix was highly nested (Fig. 5a) and the probability of finding such a highly nested matrix at random was very small ($p < 0.01$). However, the matrix temperature for all the eleven localities was rather high ($T = 12.80^\circ$), and the pattern of nestedness was disrupted by the two species *C. rufocanus* and *C. rutilus* (Fig. 5a). The genus *Clethrionomys* is only known in Japan on Hokkaido, and some of the small islands adjacent to Hokkaido, thus introducing some deviation in the general pattern of composition of the Japanese rodent assemblages. We thus computed matrix temperatures for a subset of the nine localities found within the Hondo area (all localities, except Hokkaido and Rishiri islands, Fig. 5b). For this subset, the matrix temperature value computed was very low ($T = 1.81^\circ$, $p < 0.05$). This result is a confirmation of the observations previously made on the degree of similarity between the Japanese rodent assemblages (Fig. 3). For the nine localities subset, the distribution patterns of the two voles *P. smithii* and *P. andersoni* do not follow the rule of perfect nestedness (Fig. 5b). The species *P. smithii* is present only on the largest island Honshu and on the small neighbouring island of Oki. In this case, two hypotheses, a land bridge connection between

Honshu and Oki island, or the introduction of the vole by humans onto Oki island, can be advanced. Lastly, the absence of the species *P. andersoni* in Fuji and southern Honshu might be explained by its replacement by its congeneric counterpart *P. smithii* in these localities.

Within locality patterns: community structure based on the lower incisor size and shape

The basic statistics for the three morphometric variables of the lower incisor, AP (antero-posterior diameter), R (radius of curvature) and T (transverse diameter) are listed in Table 1.

Results of the B&D test and randomisation procedure are provided in Table 2. Each test was run for each of the three size characters of the lower incisor, AP, R and T, separately. We also computed an additional variable (VOL) which represents the volume that could contain the incisor following the formula: $VOL = \pi * T * (R^2 - (R - AP)^2)$. This last variable is supposed to summarise the lower incisor size and shape, and was used to test for the effect of competition on the overall lower incisor morphology.

We did not include in the following study the species *R. norvegicus* which is represented by too small samples. Furthermore, this species is substantially larger in size than any of other Japanese murid rodents studied here.

Congruence of the two tests

When the results of the tests for each of the size characters of the lower incisor were pooled together, there was no significant correlation between the p-values obtained for the B&D test and the randomisation test (Spearman correlation coefficient: 0.35, $p = 0.12$).

The B&D test can be run for assemblages that comprise at least three coexisting species, and was thus not performed for Tane and Tsushima islands where only two sympatric species are present. In all remaining cases but one (variable T for the Hokkaido community), results of the B&D test were not significant, which indicates an absence of constant size ratios between species, for each of the size characters of the lower incisor considered. Concerning the randomisation procedure, in 8 cases out of the 40 considered, there was no overlap between species, and the test could not be performed. Results were significant in about half of the remaining cases (15 cases out of 32).

Effect of size character

Concerning the B&D test, the smallest p-values were found for size character T in four assemblages out of the seven considered. This result indicates that size

structure could be more regular for this size character than for any other character of the lower incisor. Concerning the randomisation procedure, out of the 8 cases where there was no overlap between species, four concerned the variable VOL, three the variable R, and one the variable T. This indicates that the variables VOL and R play a major role in minimizing overlaps between adjacent species, when compared to the two other size characters of the incisor, AP and T. This result is emphasised by the absence of significant result obtained for variable AP among the ten computed for this variable. Finally, significant results of the randomisation procedure concerned the variables R, T and VOL in similar proportions (four, six and five cases, respectively).

Effect of latitude and island size on community structure

We did not find any significant relation between the p-values computed for the two tests (B&D test and randomisation procedure) and the latitude and/or island size of the localities considered. In other words, communities are not better structured on small islands than on larger ones, and there is no effect of latitude on this structure. However, the randomisation procedure could not be run for some small islands, where there was no size overlap between species. The evolution on small islands might thus favour the minimisation of overlaps between species rather than the establishment of a regular size structure.

Table 1. Sample size (n), means and standard deviations of the antero-posterior diameter (AP), radius of curvature (R) and transverse diameter (T) of the lower incisor in mm.

	n	AP (mm)	R (mm)	T (mm)
Hokkaido				
<i>Apodemus speciosus</i>	18	1.426 (0.088)	9.125 (0.499)	0.808 (0.048)
<i>A. argenteus</i>	15	1.016 (0.071)	6.243 (0.411)	0.538 (0.047)
<i>Clethrionomys rutilus</i>	21	0.880 (0.091)	8.419 (0.482)	0.665 (0.054)
<i>C. rufocanus</i>	10	1.316 (0.107)	9.985 (0.557)	0.989 (0.074)
Rishiri is.				
<i>A. speciosus</i>	25	1.334 (0.112)	9.032 (0.627)	0.769 (0.046)
<i>C. rufocanus</i>	15	1.457 (0.091)	11.292 (0.406)	1.077 (0.076)
Northern Honshu				
<i>A. speciosus</i>	7	1.203 (0.135)	8.330 (0.550)	0.699 (0.095)
<i>A. argenteus</i>	12	1.030 (0.061)	6.452 (0.341)	0.571 (0.063)
<i>Microtus montebelli</i>	14	1.182 (0.101)	9.287 (0.793)	0.922 (0.093)
<i>Phaulomys andersoni</i>	15	0.996 (0.124)	8.542 (0.497)	0.769 (0.076)
Sado is.				
<i>A. speciosus</i>	31	1.289 (0.093)	8.504 (0.382)	0.782 (0.051)
<i>A. argenteus</i>	9	1.039 (0.071)	6.147 (0.213)	0.544 (0.036)
<i>M. montebelli</i>	8	1.170 (0.114)	10.037 (0.786)	1.000 (0.096)
Nikko				
<i>A. speciosus</i>	6	1.297 (0.069)	8.454 (0.328)	0.743 (0.053)
<i>A. argenteus</i>	38	1.045 (0.072)	6.409 (0.317)	0.582 (0.047)
<i>M. montebelli</i>	5	1.321 (0.092)	9.949 (0.380)	1.050 (0.080)
<i>P. andersoni</i>	17	1.119 (0.067)	9.433 (0.641)	0.959 (0.071)
<i>P. smithii</i>	20	1.036 (0.083)	7.892 (0.585)	0.813 (0.050)
Mt. Fuji				
<i>A. speciosus</i>	18	1.193 (0.121)	8.021 (0.524)	0.714 (0.068)
<i>A. argenteus</i>	44	1.018 (0.071)	6.309 (0.484)	0.547 (0.047)
<i>M. montebelli</i>	8	1.254 (0.150)	9.756 (0.619)	1.009 (0.066)
<i>P. smithii</i>	21	1.003 (0.036)	7.946 (0.518)	0.766 (0.055)
Shikine is.				
<i>A. speciosus</i>	10	1.213 (0.086)	7.923 (0.667)	0.737 (0.051)
Oki is.				
<i>A. speciosus</i>	33	1.266 (0.104)	7.924 (0.792)	0.788 (0.070)
<i>A. argenteus</i>	3	1.094 (0.025)	6.366 (0.613)	0.556 (0.053)
<i>P. smithii</i>	7	1.044 (0.061)	8.557 (0.368)	0.811 (0.044)
Southern Honshu				
<i>A. speciosus</i>	18	1.181 (0.146)	7.933 (0.715)	0.742 (0.079)
<i>A. argenteus</i>	21	1.069 (0.053)	6.575 (0.379)	0.555 (0.040)
<i>M. montebelli</i>	10	1.230 (0.108)	9.484 (0.497)	0.964 (0.061)
<i>P. smithii</i>	10	1.054 (0.121)	8.132 (0.633)	0.857 (0.068)
Tane is.				
<i>A. speciosus</i>	20	1.319 (0.144)	8.543 (0.476)	0.797 (0.081)
<i>A. argenteus</i>	3	1.135 (0.011)	6.251 (0.132)	0.559 (0.051)
Tsushima is.				
<i>A. speciosus</i>	29	1.271 (0.107)	8.577 (0.450)	0.753 (0.066)
<i>A. argenteus</i>	27	1.050 (0.062)	6.398 (0.284)	0.554 (0.037)

Table 2. Results of the Barton and David test (B&D) and of the randomisation test for four characters of the lower incisor (AP, R, T and VOL) and for ten localities. G1,n: Ratio of the smallest to the largest size ratio. Statistical significance at the 0.05 and 0.01 levels are indicated by * and **, respectively. Mean Hutchinsonian size ratios between species (Rmean) are also given for each localities and for the three characters measured on the lower incisor (AP, R and T).

Locality	Var.	G1, n	B&D p	Randomisation p	Hutchinson Rmean
Hokkaido	AP	0.310	0.254	0.226	1.179
	R	0.270	0.305	0.058	1.176
	T	0.879	0.004 **	0.002 **	1.224
	VOL	0.300	0.266	0.020 *	–
Rishiri	AP	–	–	0.857	1.098
	R	–	–	no overlaps	1.250
	T	–	–	no overlaps	1.403
	VOL	–	–	no overlaps	–
N. Honshu	AP	0.123	0.580	0.104	1.068
	R	0.097	0.650	0.123	1.135
	T	0.464	0.121	0.038 *	1.174
	VOL	0.138	0.545	0.028 *	–
Sado is.	AP	0.829	0.094	0.052	1.114
	R	0.515	0.321	0.078	1.282
	T	0.676	0.193	0.010 *	1.363
	VOL	0.689	0.184	no overlaps	–
Nikko	AP	0.102	0.485	0.090	1.066
	R	0.258	0.168	0.041 *	1.118
	T	0.368	0.078	0.143	1.162
	VOL	0.395	0.064	0.025 *	–
Mt. Fuji	AP	0.128	0.568	0.617	1.079
	R	0.038	0.844	0.027 *	1.161
	T	0.299	0.266	0.015	1.229
	VOL	0.131	0.560	0.040 *	–
Oki is.	AP	0.307	0.530	0.327	1.107
	R	0.357	0.474	0.010 *	1.162
	T	0.073	0.864	0.299	1.218
	VOL	0.165	0.712	0.260	–
S. Honshu	AP	0.096	0.654	0.052	1.052
	R	0.133	0.556	0.004 **	1.133
	T	0.395	0.171	0.018 *	1.200
	VOL	0.123	0.581	0.018 *	–
Tane is.	AP	–	–	0.214	1.158
	R	–	–	no overlap	1.366
	T	–	–	0.125	1.429
	VOL	–	–	no overlap	–
Tsushima is.	AP	–	–	0.111	1.210
	R	–	–	no overlap	1.341
	T	–	–	0.025 *	1.364
	VOL	–	–	no overlap	–

Hutchinsonian ratios

Another interesting index of community structure is the interspecific Hutchinsonian ratio, i.e. the size ratio between two species adjacent in size. These ratios were computed for each of the three size characters of the lower incisor, AP, R and T (Table 2). These ratios were not considered for the variable VOL since this variable is a nonlinear measurement. The following results are based on the mean value of the ratios computed within each community. These values fall within an interval from 1.05 to 1.43, which is very close to the interval proposed by Hutchinson (1959, from 1.1 to 1.4).

The ratios computed were the largest for size character T, while the smallest values were obtained for size character AP and intermediate values for size character

R. This variability in ratios among size characters was higher on small islands than on large ones.

Interestingly, we found negative correlations between the mean size ratio and the number of species that are present in a community. These correlations were significant for the two size characters of the lower incisor, R and T ($p < 0.001$): as diversity increases, the mean size-ratio significantly decreases. However, this relation was not significant for the size character AP ($p = 0.075$). Similarly, there were significant negative correlations between the mean size ratio and island size for all the three size characters of the lower incisor, AP, R and T ($r = -0.696$, $p < 0.025$; $r = -0.774$, $p < 0.009$ and $r = -0.791$, $p < 0.006$, respectively). This is not surprising, since the number of rodent species is strongly

affected by island size ($\text{Log}(N_{\text{spe}}) = 0.662 + 0.291 \text{Log}(\text{Area})$, $r^2 = 0.804$, $p < 0.001$).

Finally, while the diversity is reduced and the mean interspecific size ratios are increased on small islands, the total size range (difference between the mean sizes of the smallest and largest species) in a community is reduced (Fig. 6).

Discussion

Community composition

The three main biogeographic zones from Japan considered (Hokkaido and small adjacent islands, northern Honshu and small adjacent islands, and southern Honshu and small adjacent islands) are well discriminated with regard to their rodent fauna. Each of these three zones supports taxa that do not occur in other areas: *Clethrionomys* in Hokkaido, *Phaulomys andersoni* in northern Honshu, and *P. smithii* in southern Honshu.

The widespread species *Apodemus speciosus* and *Rattus norvegicus* are universal elements of the Japanese murid rodent assemblages, and are even present on very small islands such as Shikine island (4 km²). The species *Apodemus argenteus* is also very common in Japan but is absent from very small islands (Shikine and Rishiri islands), and its distribution seems thus to be limited by island area, in accordance with observations made by

Kaneko (1982). Lastly, the Arvicolinae are not well represented on small islands, when compared to the widespread species *A. speciosus*, *A. argenteus* and *R. norvegicus*. Murine rodents have thus a higher ability to colonise, establish and survive on small islands than Arvicolinae. One possible explanation is that the Murinae might exert competitive pressure on the Arvicolinae, leading them to extinction, or even preventing them from colonising small islands. In addition, the higher colonisation success on small islands among Murinae could be promoted by their more generalist habit. Crowell and Pimm (1976) similarly found that *Microtus*, due to its more opportunist (generalist) habit, had a greater success establishing on the smaller islands off the coast of Maine than *Clethrionomys*. These observations are also supported by the Quaternary fossil record from Japan. In southern Japan, the Ryukyu islands support very impoverished rodent fauna with highly endemic forms such as *Tokudaia* and *Diplothrix* which are both Murinae. However, Kaneko and Hasegawa (1995) recently recorded some Arvicolinae (the vole *Microtus*) in the Ryukyus during Late Pleistocene. It is therefore possible that both Murinae and Arvicolinae coexisted in the Ryukyus during Late Quaternary but, due to the reduction of island area during the sea level rise of the Late Quaternary, and under competitive interactions between species, only murine rodents survived on these islands.

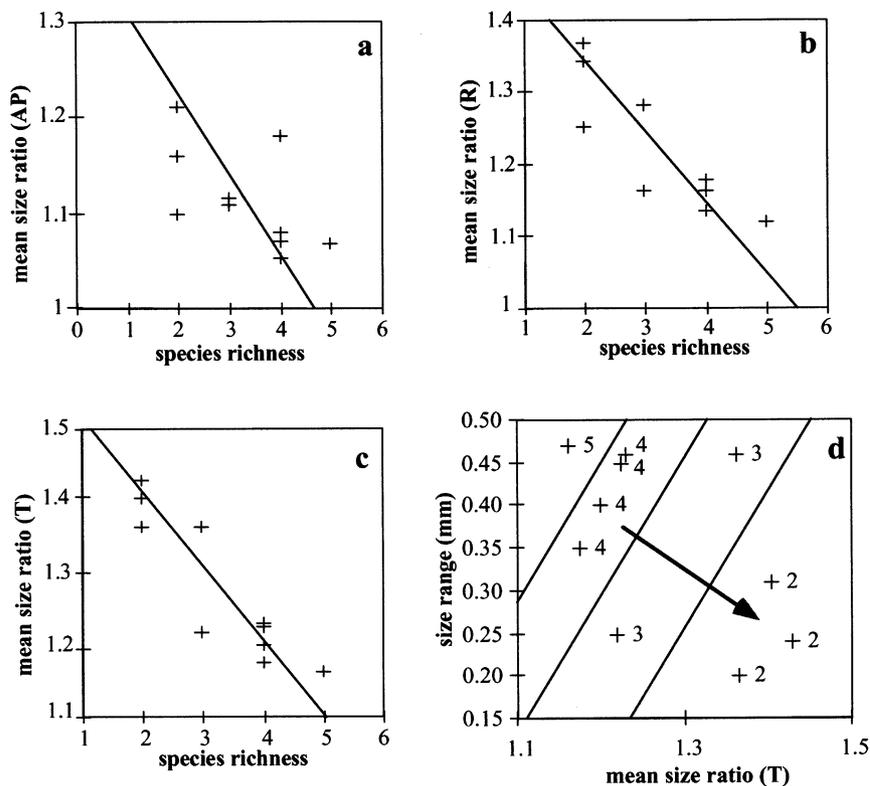


Fig. 6. a–c: relation between species richness (x-axis) and the mean size ratio between species (y-axis) in a community for the three characters of the lower incisor AP, R and T; d: relation between the mean size ratio between species (x-axis) and the total size range (y-axis) in a community for the size character T. Numbers indicate the species richness in each community. Similar representations were obtained for the characters AP and R. The arrow represents the evolution of community on islands: while diversity is reduced, the mean size ratio is increased and the total size range is decreased.

Interestingly, we can observe a replacement of the Arvicolinae in the rodent assemblages, and the following succession is observed from north to south Japan: *C. rufocanus* and *C. rutilus* in Hokkaido, *M. montebelli* and *P. andersoni* in northern Honshu and *M. montebelli* and *P. smithii* in southern Honshu (Fig. 4). In addition, *C. rutilus* is similar in size to the genus *Phaulomys*, while *C. rufocanus* is larger, and thus closer to *Microtus*. Japanese rodent arvicoline assemblages thus seem to be made up of “functional species” that play a similar role in the community, and have similar interactions with the other murine species, at least for size interactions. Many factors, from resource availability to the presence of potential competitors, can influence species occurrence within a given assemblage. Following Fox (1987), the assembly rule of small mammal communities states that “there is a much higher probability that each species entering a community will be drawn from a different functional group...until each group is represented... (Fox 1987: p. 201)”. These functional groups can be defined through differences in body size (Fox and Kirkland 1992) that reflect differences in resource utilisation and the rule implies that interspecific competition plays a major role in the assembly of communities (Fox and Brown 1993). Although Fox’s method for testing for the existence of such assembly rule for communities has been criticised (Stone et al. 1996, Wilson 1995), the Japanese murid assemblages might be competitively structured. These assemblages would thus be composed of a common pool of generalist species with broad geographic range such as *A. speciosus* and *A. argenteus*, completed by one or two more specialist arvicoline species with restricted geographic range, that are different from one locality to another.

Lastly, the nestedness analysis revealed very low temperatures for the Japanese rodent fauna. Low temperatures reflect a strong degree of nestedness, typical of relict fauna (Wright et al. 1998), and this result supports those previously obtained for the entire terrestrial mammal fauna from Japan (Millien-Parra and Jaeger 1999). The results of these analyses also strongly support the existence of several biogeographic zones in Japan. The relatively high T-value found for the eleven localities from all Japan can indeed easily be explained by the different degree of isolation of the Japanese islands. Whereas the islands from Hondo area remained isolated from the adjacent Asiatic mainland during the whole Quaternary, several land-bridge connections occurred between Hokkaido and the mainland during this period (Fujii 1990, Oshima 1990). By contrast, the high degree of nestedness found for the Hondo area indicates that the rodent fauna from this area was initially homo-geneous before its fragmentation into several islands, which is corroborated by our observations (see Fig. 5a), where Hokkaido and Rishiri islands were found to be “idiosyncratic” in a locality-wise plot of temperatures.

Community structure

The two mechanisms that led either to a regular size structure or to the avoidance of size overlaps between species act in an independent way, as there was no congruence between the two tests. In addition, we could not find any cases which illustrates the establishment of a regular size structure, at least for the incisor size. Since both upper and lower incisor sizes are highly correlated to body size and body weight among rodents (Parra and Jaeger 1998), we thus predict that such a regular structure would not be found for body size either.

Size overlaps were minimised or zero in about half of the cases studied, which indicates that the separation of size could be a more important factor than the establishment of constant size ratios, to reduce competitive interactions between species. In addition, we showed that the radius of curvature and the volume that could contain the lower incisor, that both express the incisor shape, led more often to the minimisation of size overlap. This supports Dayan and Simberloff’s (1994) contention that body size is not the best indicator of community structure, and is in accordance with results obtained for mainland rodent communities (Parra et al. 1999). It also suggests that the avoidance of interspecific competition is not only produced by size (i.e. body size) shifts but also by different adaptation of the co-occurring species to their environment. The curvature is indeed highly related to the rodent species habit (Agrawal 1967, Millien-Parra unpubl.), an increase in the radius of curvature being generally linked with an adaptation to burrowing life. In the case of the Japanese rodents, *A. speciosus* and *A. argenteus* are terrestrial species, even if they can climb well (Kaneko 1982), while the Arvicolinae *Clethrionomys*, *Phaulomys* and *Microtus* are more adapted to a burrowing life (Nowak and Paradiso 1983). In addition, the Murinae are mostly granivorous, while the Arvicolinae are specialised for a more herbivorous diet, a food habit which may well be related to the adaptation to a burrowing life: the Murinae that forage above ground, have greater access to seeds, whereas the Arvicolinae, due to their burrowing habits, have an easier access to rhizomes, and thus are more specialised for a herbivorous diet. Our results suggest that this specialisation for different food items and for different habit as well, which may provide a mechanism of coexistence for the rodent species, might be reflected in the incisor shape (i.e. the curvature) to a greater extent than in the incisor size, which is highly related to body size.

Finally, we found significant negative relationships between the mean interspecific size ratios and species richness, hence also island area. The latter result is not in accordance with the theory of limiting similarity, which implies a minimum size ratio necessary for species coexistence (Hutchinson 1959). It agrees instead

with Abram's (1983) conclusions that there is no universal limit to the similarity of competing species, and supports Simberloff and Boecklen's (1981) who found Hutchinson's rule to be invalid. Hutchinsonian ratios are rather determined by species richness, as it was found in a previous study on mainland rodent assemblages from various locations (Parra et al. 1999). The Japanese archipelago is the result of the fragmentation during Late Quaternary of a large territory into several islands, that became more or less isolated, with more or less reduced area. Thus we suggest that the evolution through time from continental to insular state, characterised by the reduction of area, can be approached by comparing islands of different areas. Using this analogy between geographical variation and evolution through time, we showed that island evolution (i.e. decrease in island area), which is accompanied by a decrease in species richness and an increase in Hutchinsonian size ratios, is also accompanied by a decrease in the total size range of the community. This could be linked to the reduction of the diversity of environmental resources (habitat and food) on islands, when compared to mainland biotas.

Conclusion

Both the composition of the Japanese rodent assemblages and their size structure seem to be mainly governed by insular trend (island area). In addition, interspecific competition is likely to be strong enough to set important constraints on community size structure.

Regarding community composition, the strong degree of nestedness of the fauna suggests the existence of selective extinctions of species leading to reduced diversity on small islands. We also observed a clinal replacement of species, from north to south, that play the same role within the community on larger islands.

Regarding community size structure, insular evolution is characterised by the minimisation of size overlaps between coexisting species, accompanied by a decrease of the whole size range and an increase of interspecific mean size ratios. No regular size structure of the Japanese rodent communities could be evidenced, and it is difficult to decide whether a regular size structure could be achieved in a longer term.

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